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REGENERATION IN ZAMIA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY LXV.

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(WITH EIGHT FIGURES)

MR. P. H. ROLFS, in charge of the Subtropical Laboratory of the United States Department of Agriculture at Miami, Florida, first called our attention to the remarkable power exhibited by mutilated stems of *Zamia floridana* of producing new shoots and roots. This cycad grows in great abundance in the neighborhood of the station, and ROLFS stated that he had seen "portions (of the stem) not larger than an English walnut" produce both shoot and root. He was kind enough to send an abundant supply of this mutilated and sprouting material, collected about February 1, 1904. The plants grow at Miami in a pure and well-drained sand, with a soil temperature standing rather uniformly at about 30° C. On April 16 ROLFS reported that the temperature of the soil one inch below the surface was 40° C.; three inches below, 38° C.; and six inches below, 35° C.

In most of the cases studied, the top of the thick stem had been cut off by the grubbing hoe, leaving the subterranean portion intact, though all of the smaller roots were lacking. Some of these stems were planted and observed at intervals. One of them, a plant about two years old, was placed in the greenhouse about February 13; the fully spread leaves soon withered, and no activity was visible for two and a half months, at the end of which time a new leaf was put forth from the bud. On June 1 the plant was removed carefully from the soil, its appearance being shown in *fig. 2*. The stem had been cut off at *x*, and had produced a new apex. Since the last planting no ordinary roots had been produced, though an upwardly directed spur 2 ^{mm} long (not shown in the photograph) indicated the beginning of one of the characteristic apogeotropic roots; and yet the young shoot was in vigorous condition.

An attempt was made to discover experimentally the possible anatomical limitations of this reproductive power, by artificial mutilations of various kinds, but probably the proper conditions for vigorous growth were not maintained; at least no results were obtained.

We have found no record of this behavior of Zamia, except in a statement made by WILLDENOW,[1] a century ago, of which the following is a translation:

> The majority of palms die as soon as their trunk is cut or even damaged. There are only a very small number of them which, like *Chamaerops humilis* and *Rhapis flabelliformis*, send out from their root new shoots; and *Cycas circinalis* is the only one which sends out shoots from its trunk when this has been cut; further, the stem of this tree gives out new roots where it finds itself in contact with the soil. The different species of Zamia may be cut up and thus multiplied artificially by cuttings, but with the exception of Cycas and Zamia no other palm survives amputation of the stem.

This power of producing new shoots and roots after mutilation is usually called "regeneration," but this term seems to have been applied primarily rather to the restoration of lost parts than to the production of a complete new structure. As a consequence of its broader application, there has been a tendency to regard the regeneration ordinarily observed in plants and in animals as of two distinct kinds; the former being nothing more than adventitious budding, the latter actual restoration of lost parts, the new structure becoming an integral part of the old. The great majority of the illustrations of regeneration in plants are cases of adventitious budding rather than regeneration in the stricter sense. We recognize the fact that the whole subject of regeneration among plants is in an inchoate condition, but perhaps the two kinds cannot be distinguished by any exact definition. Most of the cases presented in this paper are not regeneration in the restricted sense defined above, but in addition to adventitious sprouting in Zamia there also seem to be cases of direct restoration of lost parts.

In the mutilated (mostly decapitated) stems of Zamia studied, the new shoots arise most frequently from the vascular part of the central cylinder, as many as five shoots having been observed to spring from this region in a stem 3 ^{cm} in diameter, though only one shoot may occur. The vascular elements present in these shoots are continuous with the vascular tissue of the central cylinder of the parent stem.

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[1] WILLDENOW, C. L., De quelques nouveaux palmiers de l'Amérique méridionale. Mém. Acad. Roy. Berlin, 1804, p. 29.

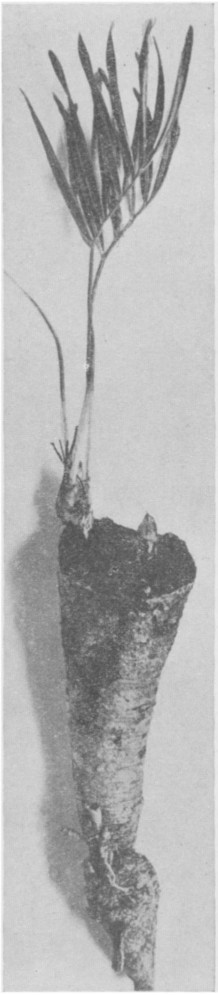

FIG. 1.—Decapitated stem showing one shoot growing from the vascular ring and one from the margin of the wounded surface. × $\frac{3}{8}$.

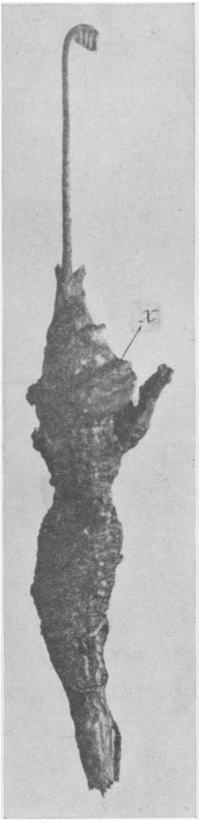

FIG. 2.—Young plant which was decapitated at *x* and has produced a new apex. × $\frac{7}{8}$.

Less frequently, the new shoots arise from the peripheral part of the wounded surface of the cortex. Both of these regions of origin may be used in the same stem, as illustrated by *fig. 1*. In the case just referred to, a distinct group of vascular strands was traced from each shoot to the vascular tissues of the central cylinder. In certain other cases no vascular connection was found, due probably to the fact that the shoots were younger and undifferentiated.

In a few cases the new structure stands directly over the central cylinder, as illustrated by *fig. 2* and observed also in much older plants. In such cases, a series of vertical sections shows that the vascular tissues of the central cylinder converge to form a dome-shaped cap underneath the restored part (*fig. 3*), that is, the whole cut end of the central cylinder regenerates, in the strict sense, the lost part being thus restored. In all other cases there is no such restoration, but the production of entirely distinct and complete structures upon the old stem. Just what conditions determine the formation of a complete new structure in the one case, and the restoration of the lost part of the old structure in another case may not be clear, but it is entirely probable that the central cylinder is more apt to be restored in young plants.

The origin of the new roots is just as variable. It is customary to think of secondary roots as arising from vascular tissue, and this was found to be true in several of the cases studied. In the case illustrated by *fig. 4*, however, no trace of central cylinder was found, the piece of stem from which the shoot springs on one side and the root on the opposite side being simply a chip from the cortex of an old stem. Between this shoot and root of cortical origin a distinct and complete vascular connection was traced, the vascular elements forming a hollow cylinder tapering at the ends (*fig. 5*). It seems certain that the decay of the "chip" in this case would uncover a completely organized new plant. In any event, from this isolated cortex new organs and new kinds of tissue have been formed, the new shoot arising from the outer edge of the cortex in the region of the cork cambium, and the root arising from a more internal region of cortex. Whether the starting of the shoot determined the root, or *vice versa*, or neither, are matters of conjecture, but a completely organized and independent new plant has been derived from isolated and relatively old cortical tissue.

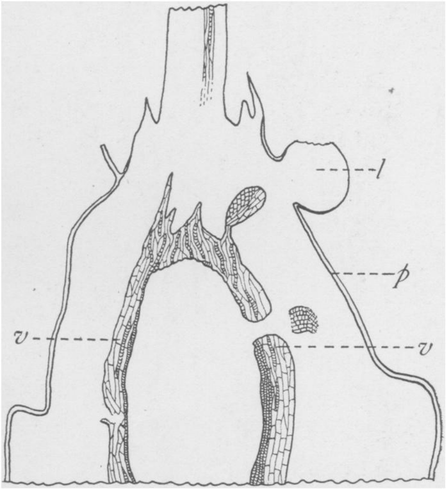

FIG. 3.—Median vertical section through apex of stem represented in *fig. 2: l*, base of leaf; *p*, periderm; *v*, vascular cylinder. × 4.

The attempt was made to determine the exact layer or tissue from which the new shoots proceed. It seems evident that regions of meristematic tissue alone are concerned, that is tissue which has either remained so or has resumed its power of cell-division; and in the ordinary cycadean stem there are at least three such active regions in addition to the growing point, namely the fascicular cambium, the pericycle, and the cork cambium. SIMON[2] finds that in regenerating root-tips the pericycle is the active layer. In Zamia the pericycle is poorly differentiated, and does not act as a secondary cambium, as is the case in Cycas and certain other cycadean genera. In the cases observed the new shoots nearly always arise from the wounded surface; and as a layer of wound-phellogen is always found beneath this surface it must be added to the list of active regions. It has been impossible thus far to secure the earliest stages in this adventitious shoot-formation, but sections through moderately young regions of this kind show the layer of callus curving outward around the base of the shoot-primordium (*fig.* 7). This suggests that the phellogen forming the callus is responsible for the initial growth of the new shoot. If this be true, a new shoot may be produced at any point of the surface covered by the callus. In fact, in the cases of Zamia before us the new shoots stand over either fascicular cambium or cork cambium, but this position seems to us to be favorable rather than essential to shoot-formation.

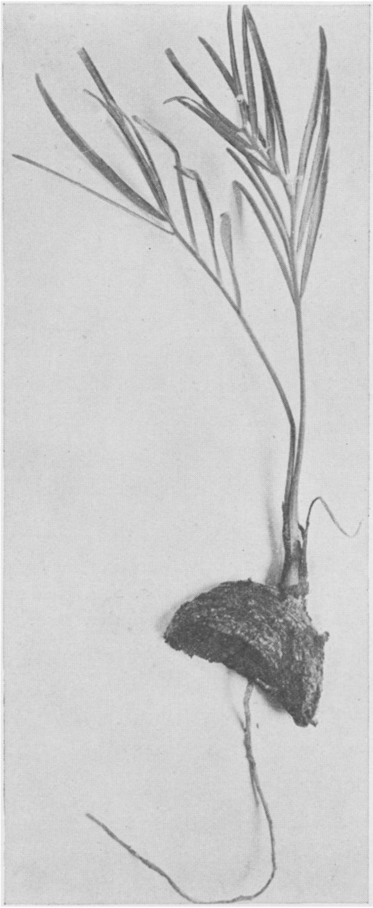

FIG. 4.—A chip from the cortex that has produced a new shoot and root. × $\frac{3}{8}$.

A case of the production of adventitious shoots from the hypocotyl of a seedling was also observed (*fig. 6*). The photograph shows a leaf arising from a bud on one side of the hypocotyl; another bud, younger than the one shown, is present on the opposite side. Anatomical examination showed that the bud contains a strong vascular strand that runs straight inwards to join one of the bundles of the hypocotyl. A layer of periderm is present just beneath the surface of the hypocotyl, and around the bud this layer bends outward to form a sort of collar (*fig. 7*). The tissues of the bud show no evidence of breaking through the cortex, as is the case with lateral roots; hence it is probable that growth of the shoot started in the phellogen. Whether the bend of the hypocotyl indicates some slight injury or not cannot be answered, at least there is no direct evidence of an injury of any kind.

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[2] SIMON, S., Untersuchungen über die Regeneration der Wurzelspitze. Jahrb. Wiss. Bot. **40**:103–143. 1904.

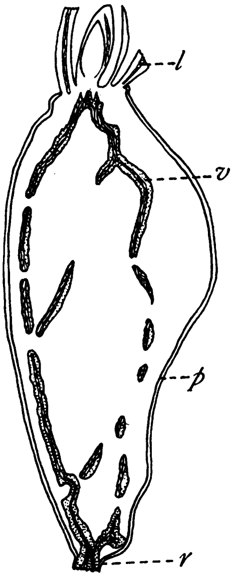

FIG. 5.—Vertical section through the piece shown in *fig. 4*: *l*, base of leaf; *p*, periderm; *r*, root; *v*, vascular cylinder. × 2.

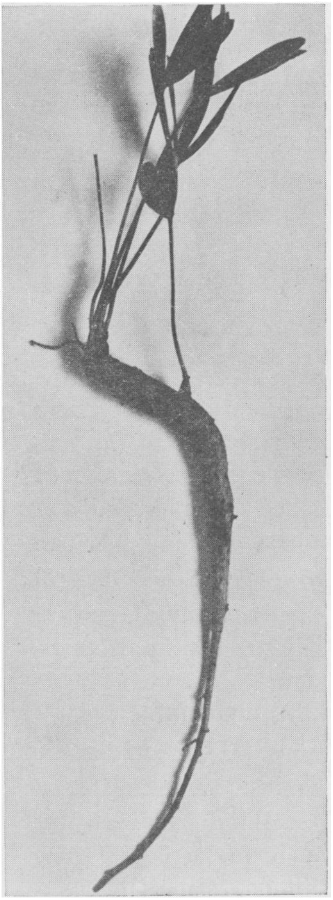

FIG. 6.—Seedling showing production of shoot from the hypocotyl. × ¾.

That a so-called polarity does not determine in this case the nature of the structure produced at each end of the mutilated stem, seems to be indicated by such a case as that represented by *fig. 8*, in which two new shoots and a root are arising from one end and a shoot from the other. It is probable that the horizontal position of the old stem is directly related to this result; and if so it would be referred to the influence of gravity.

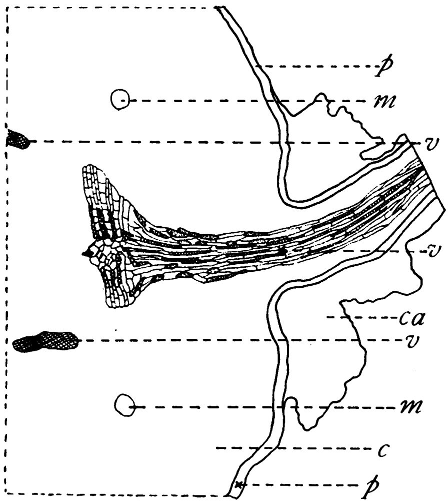

FIG. 7.—Part of transverse section through hypocotyl at level of the new shoot: *c*, cortex; *ca*, callus; *m*, mucilage duct; *p*, periderm; *v*, vascular strands. × 10.

The suggested conclusions are that in the case of the stem of Zamia the power of regeneration and of developing adventitious shoots and roots is present in all meristematic tissue; that in cases of mutilation the meristematic tissue chiefly concerned is the phellogen of the callus, that over the region of the central cylinder being more often successful than that over the cortex. This power does not seem to be localized in any definite points, such as have been called "latent buds," and which in this sense can have only a hypothetical existence; but is generally present in all meristem and expresses itself under favorable conditions. The evidence against wounding as a necessary condition for such production of new shoots is suggestive, and that against the theories of "polarity" and "latent buds" seems to be clear.

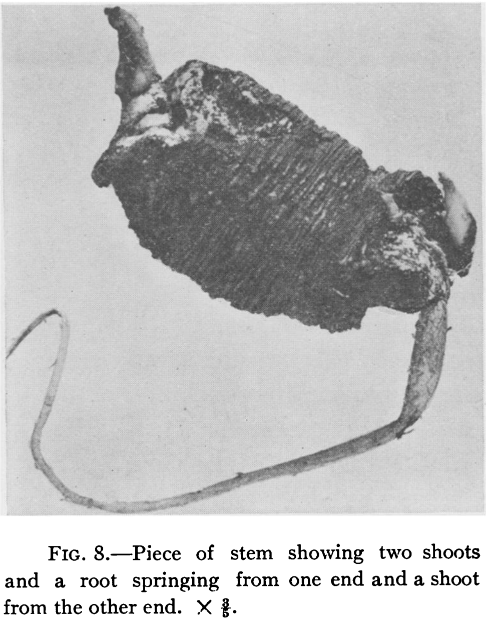

FIG. 8.—Piece of stem showing two shoots and a root springing from one end and a shoot from the other end. $\times \frac{3}{8}$.

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